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Taxonomic importance of the spermogonium*

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It is as well at the outset to disclaim all intention of treating the subject from any real knowledge of the true nature of the spermogonium. The name implies a sexual function, either active or obsolete. The similarity in structure to the pycnidia of lichens has induced many attempts to discover a similarity in function, but wholly without success. So far as known, the spermatia, which are discharged abundantly from the spermogonium, have no connection with the further development of the fungus. They may be induced to grow somewhat and bud, when placed in a nutrient solution, but no permanent structure has ever been obtained, and no parasitic connection has ever been established. So far as present knowledge extends, the spermogonium is an isolated organ with functions not yet conjectured, or whose original functions have been lost through modifications, possibly induced by parasitism.

Cytological evidence shows very distinctly that the spermogonium is an organ in no wise comparable with the uredosorus or aecidium. The spermatia, which are discharged abundantly from the spermogonium, contain each but a single nucleus, which arises by division of the nucleus in the spermatiophore from which the spermatium is abstricted, according to the researches of Sappin-Trouffy. In what manner this single nucleus is derived from the paired nuclei of the vegetative mycelium is not clear, although

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Sappin-Trouffy regards the uninucleated condition as suggestive of senility.

Waiving this inference, observe that both aecidiospores and uredospores are binucleated, and that the nuclei arise from the binucleated mycelium in the usual vegetative manner characteristic of the rusts. Both spore-forms are therefore conidia, and serve the purpose of rapid propagation of the species, being purely asexual in origin and function. This, of course, has always been assumed for the uredospores, but often denied for the aecidiospores. The work of a number of eminent cytologists no longer leaves the slightest doubt regarding the correctness of this view, and whatever degree of sexuality has been assumed for the aecidium must henceforth be abandoned.

Turning to the teleutospore we find that each cell contains two nuclei when young, but that they soon fuse in a manner highly suggestive of a sexual function. The explanation of this nuclear fusion as a genuine sexual act was first proposed by Dangeard and Sappin-Trouffy nearly ten years ago, and quite recently reaffirmed by Harper, and again very recently by Holden and Harper in an important contribution to the nuclear phenomena in *Coleosporium*. During germination the single nucleus of the teleutospore moves into the promycelium, and by dividing twice furnishes a nucleus for each of the four sporidia. In the sporidium the nucleus once more divides, but this time the process is unaccompanied by division of the cell, and thus the vegetative binucleated condition is again established, which is maintained throughout the life-cycle until the teleutospore is again reached, unless the spermogonium may be considered as introducing an interruption. However, as the uninucleated spermatia are discharged into the air and come to naught, and as the mycelium bearing the spermogonium continues the cycle by developing potentially active spores, aecidiospores for example, it is evidently permissible for our present purpose to ignore the spermogonium in tracing the nuclear cycle.

Although our knowledge of the nuclear history is not complete, yet enough has been established to permit of a reasonable inference regarding the nuclear cycle, which may be stated in brief, as follows: A fusion takes place in the teleutospore, having the physiological effect of a sexual act, and establishing the begin-

ning of the nuclear cycle. During germination the one nucleus divides into four, one for each of the four sporidia. By the time the sporidium is ready to form mycelium, its nucleus has separated into two, lying side by side, and henceforth these paired nuclei maintain an independent existence. When a new cell of the mycelium or a conidiospore is formed, each of the paired nuclei divides, half of each remaining in the old cell and half going to the new one. Thus the two associated nuclei have an independent line of descent from the time of leaving the sporidium of the germinating teleutospore until they arrive in a teleutospore again.

This account of nuclear phenomena has been given to show that the life-cycle of a rust begins with the germinating teleutospore, that is, the sporidium; that the spermogonium is a problematical organ quite *sui generis;* and that all other sorts of rust spores are of a conidial or asexual character.

The spore-forms of the rusts and the spore-bearing structures present an endless diversity, which is one of the charms of the study, and at the same time is a source of perplexing difficulties. There are, however, but two types of uredineal conidia; the aecidium and the uredo. These have received different names when presenting different aspects, and it may be well to mention the more common of these appellations. When the aecidial peridium is elongated and dehisces by numerous longitudinal slits the aecidium is called a roestelia, a form found on pomaceous hosts; when the peridium is extended and breaks irregularly we have a peridermium, which occurs on coniferous hosts; when the peridium is wanting the aecidium is called a caeoma. The uredo, when it assumes a resting state, has spores with indurated, brown walls and persistent pedicels, which are called amphispores. But throughout all the variety of forms, the aecidiospore and the uredospore retain their conidial character.

It is not always easy to decide whether a certain spore-structure is an aecidium or a uredo, and it would not be difficult to point out many instances where they are confused in the recent writings of some of the most eminent uredinologists, were it not both ungracious and uncalled for to do so. In general they may be distinguished by the spores of the aecidium always being pro-

duced in chains, and those of the uredo being produced singly on evident pedicels, except in case of the genera of the *Coleosporieae* and *Chrysomyxeae*, where they as well as the aecidiospores are in chains. In all cases the aecidium is developed before the uredo in point of time.

This brings us to a consideration of the succession of spore-forms in the cycle of development. In the first place it may be said that the order is invariable. The germinating teleutospore gives rise to the sporidium, from the mycelium of which is produced first the spermogonium, then the aecidium, and later comes the uredo, and then the teleutospore completing the cycle. Either the aecidium or the uredo may be omitted from the cycle of development, or both may be omitted, as occurs in many species, but the spermogonium is rarely omitted, and the teleutospore with its sporidium never. The developmental order and the suppression of spore-forms may be represented in four series. By using the Roman numerals I, II and III for aecidia, uredo and teleutospore respectively, the cipher for the spermogonium, and the letter *y* for the sporidium, the series may be shown in tabular form, or they may be represented diagrammatically. By far the largest number

SUCCESSION OF SPORE-FORMS

A. Complete series.	B. Uredo wanting.	C. Aecidia wanting	D. No uredo or aecidia.
y	*y*	*y*	*y*
o	o	o	o
I	I	—	—
II	—	II	—
III	III	III	III

of species are illustrated by the first series, having all spore-forms present; a much smaller number by the second series, having the uredo suppressed; and a still less number by the third series, having the aecidium suppressed. The fourth series, with both conidial forms suppressed, claims many species, however, and possibly more than either the second or third. In each of the four series the spermogonium is sometimes suppressed. Very little attention has been given to the presence or absence of the spermogonium, however, and the recorded data bearing upon the matter are extremely meager. At present it is unwise to venture an opinion whether the non-appearance of this structure in any

species is due to conditions of growth, to adaptations extending over a long period, to reduction as the result of parasitism, or to specific variation. All that can be said is that it seems probable that in some species the spermogonium is wholly wanting, but that in the great majority of species it is present.

The general conception of the spermogonium is, I venture to say, that of a minute structure necessarily accompanying the aecidium, although in some exceptional cases it may occur in connection with the other spores. This view is the outgrowth of

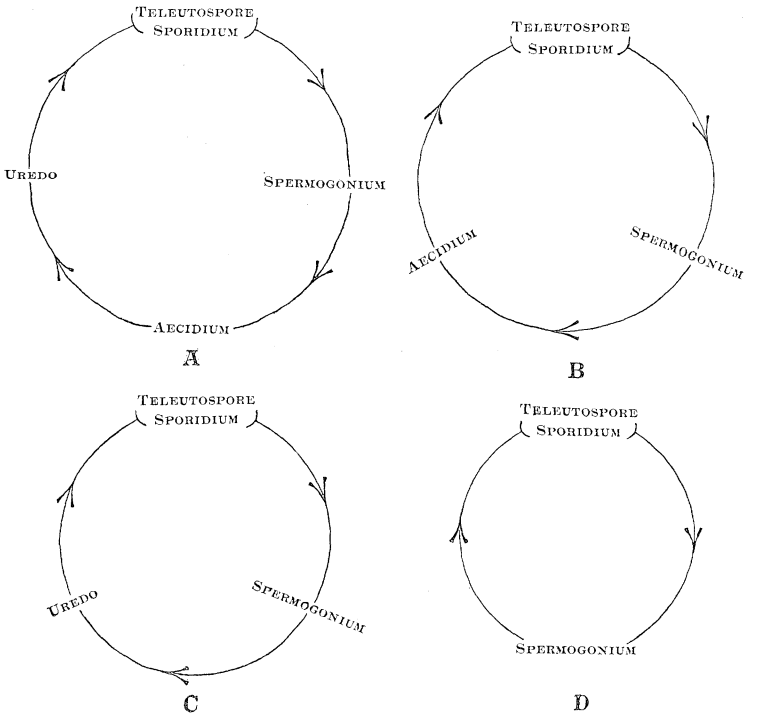

FIG. 1. Diagrams to illustrate the succession of spore-forms in a cycle of development; **A,** all spore-forms present; **B,** uredo-stage suppressed; **C,** aecidium-stage suppressed; **D,** both uredo and aecidium suppressed. The suppression of spore-forms sometimes extends also to the spermogonium.

the teaching of DeBary. The spermogonium was first described by Tulasne in 1851, and believed to be the male organ of reproduction. In 1866 DeBary published his epoch-making work on the morphology and physiology of the fungi, and in this he says

that with a few exceptions the spermogonia are the constant accompaniment and precursors of the aecidia, and that this points to a sexual relation between them (page 169). In the second edition of the work in 1865 this statement is elaborated, and has been made familiar to English-speaking botanists through the translation of 1887 (page 276). As exceptions DeBary recorded in his earlier work that in cultures of *Endophyllum Sempervivi*, which usually produces spermogonia, repeated generations of aecidia occurred without a trace of spermogonia. In 1879 Schröter observed that aecidia of *Uromyces* on *Ervum* and of *Puccinia* on *Galium Aparine* are produced throughout the warm months, but that only the first generation in springtime is accompanied by spermogonia. In 1891 Barclay made observations upon a *Uromyces* on *Jasminum sempervivum* in India which produced aecidia accompanied by spermogonia when sporidia from germinating teleutospores were sown, but which produced aecidia unaccompanied by spermogonia when aecidiospores were sown. In 1895, in an article on rust-fungi with repeated formation of aecidia, Dietel added to the number of such species, coming to the conclusion that, in those species of *Uromyces* and *Puccinia* which form aecidia and teleutospores but no uredospores, the aecidiospores have the power again to bring forth aecidia, provided the mycelium is not perennial in the host. He called the aecidia arising directly from germination of teleutospores "primary aecidia," and those arising from germination of aecidiospores "secondary aecidia," and noted that spermogonia were usually absent from the latter. The same descriptive method has since been employed with the uredo; the primary uredospores being those which arise first accompanied by spermogonia; and the secondary uredospores, often of a different size and appearance, being those which come later without spermogonia.

Going back to the statement of DeBary, which is also the accepted view of every subsequent writer, that usually the spermogonia are the accompaniment and precursors of the aecidia, or in a few cases, we may add, of the uredo, we are now in a position to point out that the statement is only true in a superficial way, and in reality is misleading. Every one who has made cultures of the rusts knows that, in about a week after sowing the germinat-

ing teleutospores, there will appear spermogonia, without any regard to the kind of spore that is to follow. The spermogonium is clearly the first fruiting structure to arise in the cycle of development, that is, the first to follow nuclear fusion, which we may assume to be the sexual act. If we are, therefore, to regard the spermogonium as having any necessary association with other spore-forms, it must be with what precedes, that is, with the sporidium of the teleutospore, rather than with the conidia which follow. That this is physiologically as well as morphologically true is shown by the fact that the conidia closely following the spermogonia are usually larger and in many ways more vigorous than those conidia which arise from the germination of conidia, and thus are further removed from the reinvigoration of nuclear fusion. In some species with primary and secondary uredo, as for example, *Puccinia suaveolens*, and *Phragmidium Potentillae* on *Potentilla Canadensis*, the primary uredo when fresh can be told at a glance by the richer coloration and the larger and more compact sorus. It may be argued that the reason why the primary uredo is larger and stronger is because of its association with the spermogonium, which may be true, but if so, the explanation of it can not now be shown or even clearly conjectured. It is evident, however, that assuming the nuclear fusion in the teleutospore to be an invigorating process, and that position seems fairly unassailable, the effect of the fusion must be most marked in the earliest fruiting-bodies, and grow less and less the greater the number of removes, and hence the difference between the primary and secondary uredo.

Before reaching the chief feature of this paper there is one more phase of cyclar development that should be presented. It is the relation of the repeating conidia to the succession of spore-forms. The incompleteness of knowledge of full life-histories is especially felt in making generalizations regarding this feature of development. All that can be claimed is probable correctness. Both tabular and diagrammatic methods of illustration may be employed as before. When the uredo occurs in the series, the uredospores by germination give rise to a mycelium that at once produces more uredospores, and these may repeat the process, and so on indefinitely, or until the favorable season for growth

draws to a close, in this manner widely distributing the species. If no uredo occurs in the series, the aecidiospores often possess the power of repetition; and if neither uredo nor aecidia occur, the teleutospores may act in the same way, as in the numerous species of the *Lepto-Uredineae*.

It is worthy of note that in a complete series of spore-forms there is but one generation of aecidia, and that the mycelium bearing the aecidia does not continue, as a rule, to live and produce uredospores, but comes to an end with the fruiting of the aecidia. The fungus is then re-established by aecidial germination. Thus the development is thrown into two hemicycles. One may incidentally observe that, except as an aid to heteroecism, there appears no evident advantage to the fungus in possessing two conidial spore-forms. All the work of dissemination is equally well done by either one of the two forms, acting alone.

SUCCESSION OF SPORE-FORMS.

A. Complete series	B. Uredo wanting.	C. Aecidia wanting.	D. No uredo or aecidia.
y	*y*	*y*	*y*
o	o	o	o
I	**I**	—	—
II	—	**II**	—
III	III	III	**III**

The repeating spore-forms are in heavy type.

An observation more pertinent to our inquiry is, that the spermogonium occurs but once in the cycle, not being repeated with each generation of repeating aecidia or uredo. In case the teleutospore takes on the conidial function it is uncertain whether the spermogonium is repeated with each summer generation or not. In *Puccinia Malvacearum*, and similar *Lepto-Uredineae*, the spermogonium seems to be wholly suppressed, even with the first generation in spring. It is unnecessary, however, for the purposes of this paper either to decide or to discuss this doubtful point.

After this rather tedious exordium I am prepared to make the first of two statements regarding the taxonomic value of the spermogonium: to record its presence, and the spore-generation with which it is associated, gives valuable information regarding the probable length of the cycle. By referring to the last diagrams it will be clear at a glance, that if spermogonia and uredospores

are found arising from the same mycelium, aecidia do not occur in the cycle; and if spermogonia and teleutospores are found arising from the same mycelium, there are neither uredo nor aecidia in the cycle. If we read a diagnosis in which only teleutospores are

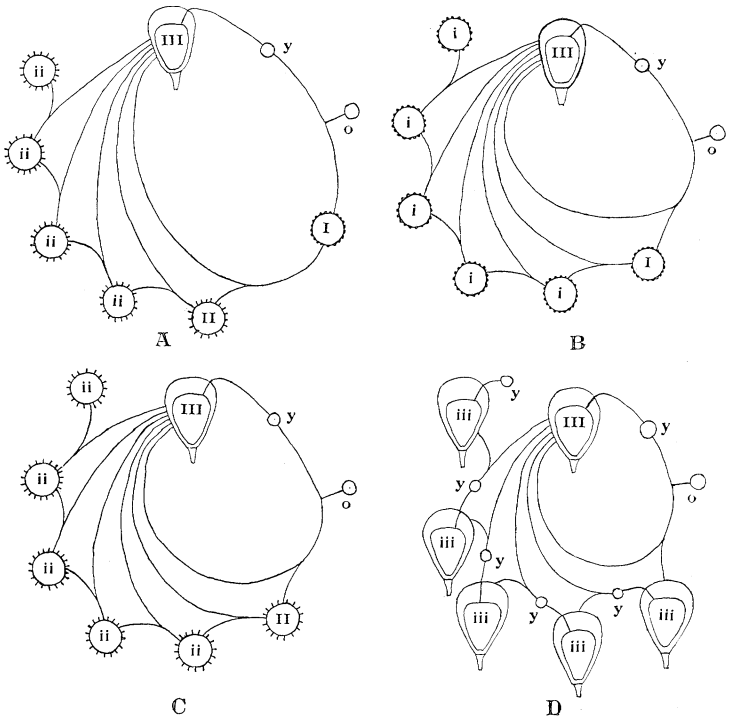

FIG. 2. Diagrams to illustrate the succession of spore-forms, the continuity of the mycelium, and the repeating generation, within a cycle of development.

Curved lines represent mycelium; when the lines branch, two kinds of spores are borne by the same mycelium, usually one succeeding the other in point of time; **III**, primary teleutospores; **iii**, secondary or repeating teleutospores; **I**, primary aecidia; **i**, secondary or repeating aecidia; **II**, primary uredo; **ii**, secondary or repeating uredo; **y**, sporidia; **o**, spermogonia.

A, complete cycle of development, the repeating generation being the uredo; **B**, cycle with the uredo suppressed, the aecidium being the repeating generation; **C**, cycle with the aecidium suppressed, the uredo being the repeating generation; **D**, cycle with both aecidium and uredo suppressed, the teleutospore being the repeating generation.

mentioned, there is no way of judging whether the rust also possesses aecidia and uredo or not, unless it is stated that the teleutospores germinate immediately upon maturity, when usually, although not invariably, other spore-forms are absent. To mention

that spermogonia are directly associated with the teleutospores sets the matter at rest. The same is true when they are associated with the uredo. But when they are associated with the aecidia, the case is somewhat different. Only in instances where teleutospores and aecidia arise from the same mycelium, and immediately adjoining, can it be told from a specimen in hand that the cycle is without uredospores.

It should be mentioned, that it is not to be inferred that when spore-forms are suppressed, all trace of them is lost. On the contrary, when the uredo-form is suppressed, a few uredospores are often found intermixed with the teleutospores; and when both aedicia and uredo are suppressed, a few peridial cells and uredospores may occur in the teleutosori, reminders of two lost conidial generations.

My second statement regarding the taxonomic value of the spermogonium is, that position, form, color and size, are characters worth recording, but have only minor value, as the range of variation is slight. The spermogonium is usually a flask-shaped body, averaging 100–150 μ in diameter, formed immediately beneath the epidermis. The narrow neck protrudes through the epidermis, in order to discharge the spermatia into the air. Sometimes, especially in certain species of rusts parasitic upon *Ranunculaceae*, *Anacardiaceae*, *Rosaceae* and *Caesalpiniaceae*, the spermogonium is formed in the upper epidermal wall, just beneath the cuticle, and is then more or less hemispherical or conical. Intermediate forms sometimes occur, but the variation is usually inconsiderable. The position of the spermogonia in relation to the accompanying spore-form is also worth noting. The two structures are usually upon opposite sides of the leaf bearing them, but occasionally both are on the same side. The spermogonia sometimes occupy a small limited area, with the conidiosori on the opposite side of the leaf, or encircling them on the same side; or they may be scattered thickly or sparsely over large areas intermixed with the conidiosori, or opposite them.

The purpose of the paper has now been attained, if the two-fold value of including information about the spermogonium in every descriptive account of a rust has been made clear. Spermogonial characters probably have little or no generic value, but

their specific value is considerable, first as an indication of the nature of the life-cycle, and secondly in furnishing positive characters for identification. Incidentally it has been explained that the common conception of the spermogonium as an accompaniment of the aecidium, or other spore-forms, is incorrect and misleading. The spermogonium should rather be considered a fixed structure accompanied by some other spore-form as a rule, but in no wise dependent upon the same.

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